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## Transformations at high latitudes

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## **TRANSFORMATIONS AT HIGH LATITUDES: WHY DO RED KNOTS BRING BODY STORES TO THE BREEDING GROUNDS?**

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## SHORT COMMUNICATIONS

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### MANDIBULAR BOWING AND MINERALIZATION IN BROWN PELICANS

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**Abstract.** Brown Pelicans (*Pelecanus occidentalis*) plunge dive into water to capture fish with highly distensible pouches. During prey capture, the pouch may expand to hold 11 L of water and the mandibular rami may bow from a resting position of 5 cm to over 15 cm. We compared mineralization of two bending regions of the mandible with a nonbending region, and examined cross-sectional morphology to determine if mineral content and shape play a role in mandibular bending. A rostral bending zone, adjacent to the mandibular symphysis, possessed only about 20% mineral content, significantly less than the lateral bending zone and the rigid caudal mandible, both comprised of over 50% mineral content. Additionally, the rostral zone was solid in cross section, facilitating bending, whereas the lateral zone was made up of bones joined by connective tissue. This latter morphology permits movement between the bones even though there was relatively high mineralization. We suggest that mineral content may be an overlooked component to cranial kinesis in birds.

**Key words:** Brown Pelican, cranial kinesis, feeding, jaw mechanics, *Pelecanus occidentalis*, streptognathism.

#### Arqueamiento y Mineralización de la Mandíbula en *Pelecanus occidentalis*

**Resumen.** Los pelícanos *Pelecanus occidentalis* se zambullen en el agua para capturar peces utilizando bolsas bucales muy distensibles. Durante la captura de la presa, la bolsa bucal se puede expandir para contener hasta 11 litros de agua y las ramas mandibulares se pueden arquear desde una posición de descanso de 5 cm hasta más de 15 cm. En este estudio, comparamos la mineralización de dos regiones mandibulares que se arquean con una región rígida que no se arquea y examinamos la morfología transversal para deter-

minar si el contenido mineral y la forma desempeñan una función al arquear la mandíbula. Una zona de doblado rostral adyacente a la sínfisis mandibular posee un contenido mineral de aproximadamente el 20%, lo que representa una mineralización significativamente menor que la de la zona lateral de doblado y la sección caudal rígida de la mandíbula, las cuales contienen más de un 50% de minerales. Adicionalmente, la zona rostral tiene una sección transversal sólida que facilita su arqueamiento, mientras que la zona lateral está compuesta de huesos unidos por tejido conectivo. Esta última morfología permite el movimiento entre los huesos aunque exista una alta mineralización. Sugerimos que el contenido mineral puede ser un componente de la quinesis cranial de las aves que es frecuentemente ignorado.

Brown Pelicans (*Pelecanus occidentalis*) dive into water for fish from altitudes of 9–16 m (Allen 1923), often attaining speeds of up to 18 m sec<sup>-1</sup> before water impact (Johnsgard 1993). Their gular pouches are highly distensible, and can hold up to 11 L of water (Schreiber et al. 1975). Schreiber et al. (1975) estimated that when the mandibles bow (from a resting position of about 5 cm apart to over 15 cm apart) the opening created is approximately 500 cm<sup>2</sup>. This bowing, termed streptognathism, is well-developed in birds that are able to swallow large objects (Judin 1961, Zusi 1993), such as pelicans. Mandibular bowing in pelicans may be produced by: (1) passive interaction between the water and the flexible mandibles (Schreiber et al. 1975), (2) contraction of pouch musculature (i.e., genioglossus muscle) pulling the chin caudally (Johnsgard 1993), or (3) action of the pterygoid musculature acting on the internal process of the mandible (Böker 1938, Judin 1961, Burton 1977).

When bowed, the mandible has two distinct pairs of bending zones: one pair on either side of the mandibular symphysis, and another occupying approximately the rostral two-thirds of the mandible (Fig. 1). Bending zones within the avian skull are typically described as being thin bony regions (Gussekloo et al. 2001) or multilayered bony laminae (Bühler 1981). Studies of

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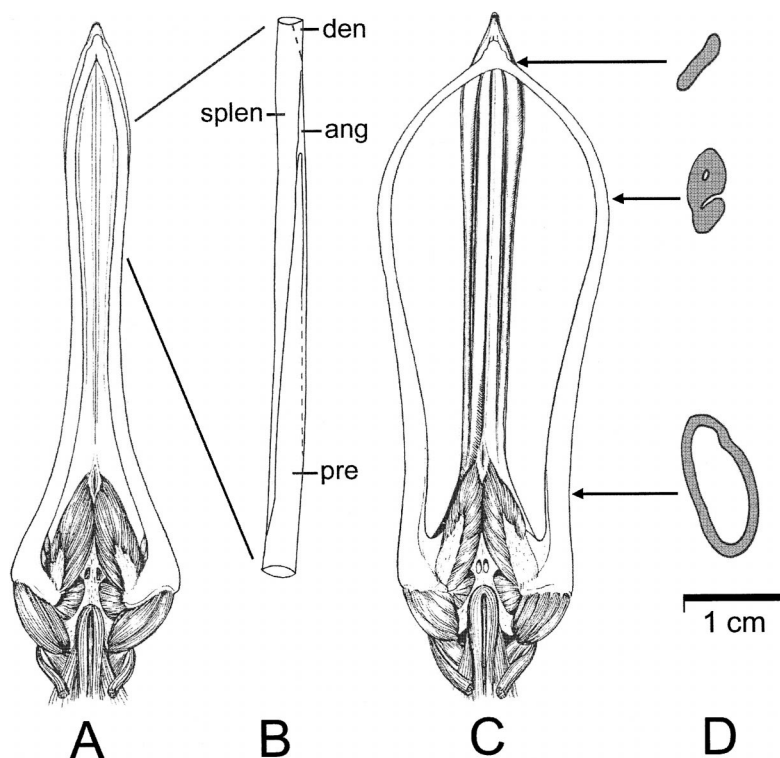


FIGURE 1. Mandibular bowing in the Brown Pelican (*Pelecanus occidentalis*). (A) Ventral view of pelican head and lower jaw in resting position, pouch removed (modified from Böker [1938]). (B) Medial view of left mandible, showing lower jaw bones that make up the "leaf spring" area of the lateral bending zone. ang = angular; den = dentary; pre = prearticular; splen = splenial. (C) Ventral view of pelican head and lower jaw in bowed position, pouch removed (modified from Böker [1938]). (D) Cross sections through the three lower jaw regions studied: top, solid rostral bending zone; middle, syndesmotomic lateral bending zone; bottom, caudal nonbending zone (scale = 1 cm).

avian cranial kinesis typically focus on the upper bill and not the lower jaw, though there have been exceptions (Judin 1961, Bock and Kummer 1968). Judin's (1961) detailed paper on the lower jaw describes a complex syndesmosis (a type of joint in which bones are joined by connective tissue) that accounts for lower jaw bowing in gulls and other species, including pelicans. In this paper, we examined the bending of the Brown Pelican lower jaw, and show that both mineral content and bone shape contribute to the high degree of bowing observed when this species dives into the water for food.

#### METHODS

Fresh specimens of four adult Brown Pelicans were obtained from the North Carolina State Museum of Natural History, Raleigh, NC, and from Pelican Harbor Seabird Station, Florida. Mandibles were removed, stripped of their keratinous rhamphothecae and underlying connective tissue, and dried. Cross sections were determined using a Siemens (BMI Medical, Lake Barrington, Illinois) Volume Access Multirow CT scanner with a field of view of  $1024 \times 1024$  pixel images at McKay-Dee Hospital in Ogden, Utah. These images

were used to resolve cross-sectional shapes and to calculate second moments of area. The latter gives a measure of how bendable a beam or tube is. It takes into account the relative height to width as well as the thickness of the tube wall and its distance from the central axis (Panjabi and White 2001). Calculations were made on ellipses that closely approximate the shape of each jaw region.

Mineral content of three mandibular regions was determined by ashing fragments of dried bone from areas along the length of the lower jaw: the rostral bending zone adjacent to the symphysis, the syndesmotomic lateral bending zone, and the caudal non-bending part of the mandible (Fig. 1C, D). Small pieces of bone (Mean mass =  $0.12 \pm 0.10$  g) were weighed using a Mettler (Columbus, Ohio) PE 360 milligram balance to determine initial mass ( $M_0$ ) and then placed in a ceramic crucible. The samples were individually heated with a bunsen burner to over  $600^\circ\text{C}$  for periods of 20 min, after which all of the organic material in the bone should have been burned away, leaving only mineral behind. Once it was cool enough to handle, the crucible was weighed and its (pre-ashing) mass was sub-

TABLE 1. Mean mineral content (%) and number of samples (*n*) from each region of the mandible of four Brown Pelican individuals. Note that for the rostral zone, samples consisted of a single fragment from both sides of each mandible.

Individual	Mandibular Region					
	Rostral zone		Lateral zone		Caudal zone	
	Mineral content (%)	<i>n</i>	Mineral content (%)	<i>n</i>	Mineral content (%)	<i>n</i>
1	22.1	2	50.2	9	48.5	4
2	19.6	2	52.9	17	57.5	3
3	15.4	2	50.7	8	61.7	3
4	23.3	2	55.0	7	52.5	3

tracted out to obtain the bone fragment's final mass (*M*). The percent mineral content was determined using the following equation (Papadimitriou et al. 1996):

$$\text{Mineral content (\%)} = (MM_o^{-1}) \times 100.$$

Mean mineral content was calculated for each region per mandible, and then a grand mean was calculated for each region across the four individual mandibles (Table 1). A one-way analysis of variance (ANOVA) was conducted to compare mineral content among regions (SPSS Inc. 2001). An *a priori* contrast using the *t*-statistic was used as a *post-hoc* test to compare the mineral content of the rostral bending zone to the other mandibular regions. Alpha levels of 0.05 were considered significant and values are reported as mean  $\pm$  SD.

## RESULTS

We found specializations for two distinct bending zones within the pelican lower jaw. The rostral bending zone, directly adjacent to the symphysis, is narrowly elliptical in shape and solid in cross section (Fig. 1D). This very small region only 2–3 mm long has a second moment of area of 0.29 mm<sup>4</sup>. Ash analysis determined that the rostral bending zone is an area of very low mineralization (20%  $\pm$  4% mineral content, Fig. 2).

Occupying the rostral two-thirds of the mandible are lateral bending zones, which are composed of syndesmoses between the dentary and splenial bones, rostrally, and the prearticular and angular bones, caudally (Fig. 1B). This region is generally oval in cross sectional shape with small spaces corresponding to the location where connective tissue joins the bones, as well as an internal space between the bones. This region has a second moment of area of 25.1 mm<sup>4</sup> and a mean mineral content of 52  $\pm$  2% (Fig. 2). The caudal one-third of the mandible is oval, rigid, and hollow with a second moment of area of 493.6 mm<sup>4</sup>. Its mineral content is similar to that of the lateral bending zone (56  $\pm$  5%; Fig. 2). Our data support the hypothesis that mineral content differs among regions ( $F_{2,9} = 90.3$ ,  $P = 0.0001$ ). The contrast follow-up test indicates that the rostral bending zone has a significantly lower mineral content than the other regions ( $t_{1,9} = -13.4$ ,  $P = 0.0001$ ).

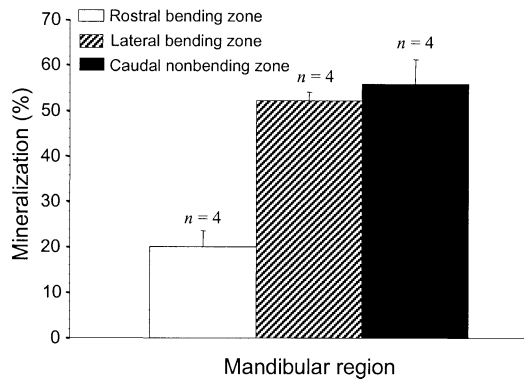


FIGURE 2. Average mineral content ( $\pm$  SD) of the rostral bending zone, lateral bending zone, and caudal nonbending zone from Brown Pelicans.

## DISCUSSION

Although the mechanism of pouch expansion and mandibular bowing of the Brown Pelican is a subject that has been studied very little, there are conflicting results. Böker (1938), Judin (1961), and Burton (1977) suggested that the pouch expands due to contraction of the pterygoid muscles. Schreiber et al. (1975) explained that pouch expansion is likely passive, and is due to the interaction of the jaws with the water. Lastly, Johnsgard (1993) suggested that a (unspecified) pouch muscle could bow the jaws by pulling the chin caudally.

The mandibular bending zones are clearly essential to the Brown Pelican feeding apparatus. Judin (1961) described the morphology of the syndesmotomic lateral bending zone in gulls and compared it with many other species. He noted that three groups of birds could be distinguished based on this characteristic of the lower jaw: species with the lower jaw divided into cranial and caudal parts connected by syndesmotomic sutures capable of bending (e.g., gulls, pelicans), species with the bony elements of the lower jaw connected by syndesmoses but arranged such that no bending is possible (e.g., ostriches), and species whose lower jaw lacks sutures (e.g., raptors, parrots, passerines). Judin (1961) concluded that streptognathism probably evolved convergently many times within birds.

Bühler (1970) described in great detail the mechanism for lower jaw bowing in goatsuckers (Caprimulgidae) in which there are two bending zones: an "anterior intramandibular joint" (our rostral bending zone) and a "posterior intramandibular joint" (our lateral bending zone). Bühler (1970) describes the anterior intramandibular joint as a "kinetic synostosis" [a union of two bones to form a single bone] caudal to the symphysis and the posterior intramandibular joint as a "well-known hinge joint." The anatomical arrangement of bending zones in the Brown Pelican is somewhat similar to that of goatsuckers, although the extreme rotation seen in *Caprimulgus* does not occur in *Pelecanus* (Zusi 1993), nor is jaw depression linked to bowing (Judin 1961).

The decreased mineralization and solid cross section of the rostral bending zone make it extremely bendable. Bones typically function to resist bending, but mineral content and shape can affect the degree to which bones can bend (Currey 1984, 2002). Mineral content is correlated with the mechanical properties of bone, and it is well known that decreased mineral content makes a bone more flexible and less likely to break (Currey 1979, 1984, 2002, 2003, Papadimitriou et al. 1996). For example, the proximal and middle phalanges of bats (*Tadarida brasiliensis*) have a mineral content of about 30 percent; distal phalanges have no mineral content and are cartilaginous (Papadimitriou et al. 1996). These low mineral levels are interpreted as being useful for flexibility in wingtip deformation during flapping flight. Similarly, the low mineral content of deer antlers (59%) is viewed as an adaptation to resist breakage during fighting (Currey 1979, 2003).

In addition, shape plays an important role in the mechanical properties of bones. It is well known that given a tube and rod of similar material and equal mass, the hollow rod will resist bending more than a solid rod (McGowan 1999). The rostral bending zone, in addition to being only about 20 percent mineral content, is solid in cross section, and taller than wide, thus facilitating lateral bending (Vogel 1988). This is again similar to the distal phalanges of bats that are also solid in cross-section (Swartz 1998). Even though the rostral bending zone has only about one-third of the cross-sectional area (of bone) of the hollow caudal region, its second moment of area is still about 500 times less! Since the rostral bending zone is also 2.5 times less mineralized, this zone is even more bendable than it would be based on shape alone.

Mandibular bending is also not restricted by the presence of the overlying keratin. The keratin that overlies the rostral bending zone is much more skin-like and not at all like typical rhamphothecal keratin. Homberger and Brush (1986) described different categories of avian keratins based on mechanical properties and molecular weight of the keratin monomers. We suggest that the keratin overlying the rostral bending zone is likely to be more similar to skin keratin in its molecular weight.

The lateral bending zone is morphologically unlike the rostral bending zone. It is comprised of syndesmoses of the dentary, splenial, prearticular, and angular bones. Both Judin (1961) and Bühler (1981) reported that this bending zone is made up of bony laminae interspersed with connective tissue and Judin (1961) described how this separation of bones "increases space" within the pelican's zone of flexibility and allows this area of the mandible to bow. These bones are solid in cross section, and have a mineral content of about 52 percent. This syndesmotomic joint permits these bones to move relative to one another, much like a leaf-spring functions. Despite the relatively higher mineral content of this region, this movement of lower jaw bones contributes to the high degree of lateral bowing seen during pelican feeding.

In conclusion, we have described how very low mineralization and shape facilitates bending in the lower jaw of Brown Pelicans. Future work needs to

determine the type of keratin overlying the rostral bending zone, and to determine if reduced mineralization is associated with bending zones in both the lower jaws and skulls of other bird species.

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## TRANSFORMATIONS AT HIGH LATITUDES: WHY DO RED KNOTS BRING BODY STORES TO THE BREEDING GROUNDS?

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**Abstract.** We examined changes in body composition of Red Knots (*Calidris canutus islandica*) following arrival on their High Arctic breeding grounds at Alert, Ellesmere Island, Canada. Knots arrived in late May and early June with large fat and muscle stores. In the next two weeks, fat and protein stores (pectoral muscles) declined, while increases occurred in gizzard, proventriculus, gut length, heart, liver, and possibly gonads. Most stores were used before egg laying occurred and were therefore not available for egg formation. Early development of ova in some females suggests that body stores may be incorporated into the earliest eggs. While stores may be used for survival when conditions are difficult after arrival, their rapid loss and the concomitant increase in other organs suggests that a major function may be to facilitate a transformation from a physiological state suitable for mi-

gration to one suitable, and possibly required, for successful breeding.

**Key words:** body stores, *Calidris canutus*, High Arctic, migration, phenotypic flexibility, Red Knot, shorebirds.

### Transformaciones a Altas Latitudes: ¿Por qué *Calidris canutus islandica* Lleva Reservas Corporales a los Sitios de Nidificación?

**Resumen.** Examinamos los cambios en la condición corporal de individuos de *Calidris canutus islandica* luego de que éstos llegaran a sus territorios reproductivos a altas latitudes en el Ártico en Alert, isla Ellesmere, Canadá. Los individuos de *C. c. islandica* llegaron a fines de mayo y comienzos de junio con grandes reservas de grasa y músculo. Durante las dos semanas siguientes, las reservas de grasa y proteína (músculos pectorales) disminuyeron, mientras que la molleja, los proventriculos, el largo del intestino, el hígado y posiblemente las gónadas aumentaron de tamaño. La mayoría de las reservas fueron usadas antes

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del período de puesta de huevos, por lo que éstas no estuvieron disponibles para la formación de los huevos. En algunas hembras, el desarrollo temprano de los óvulos sugiere que las reservas corporales pueden ser incorporadas en los primeros huevos. Si bien las reservas pueden ser usadas para sobrevivir en el momento de la llegada cuando las condiciones son difíciles, su rápida pérdida y el aumento concomitante en otros órganos sugiere que una de las funciones principales de las reservas podría ser facilitar la transformación de un estado fisiológico apropiado para la migración a un estado apropiado y posiblemente requerido para la reproducción exitosa.

Shorebird species that migrate between High Arctic breeding grounds and more southerly temperate wintering areas undergo remarkable morphological changes during the course of their travels (Piersma 1998). These journeys may involve several long-distance flights, each of which involves cycles of fuel deposition and expenditure. Whereas it was once thought that all of the mass increase in birds before migration consisted of fat (Odum et al. 1964), more recent work has shown that changes in body composition are much more subtle and complicated, and may involve a suite of changes in the relative sizes of various organs and tissues which are highly adaptive in preparing the birds for the impending flight (Piersma 1990, Piersma and Gill 1998, Piersma et al. 1999). For shorebirds, typical morphological changes involve reduction in the size of "nutritional organs," such as the stomach and intestines, and increases in the "exercise organs," such as the pectoral muscles and heart, that power flight (Piersma and Gill 1998, Piersma et al. 1999). Calcium also appears to be accumulated by females (only) during the final stopover on northward migration (Piersma et al. 1996). During the flight, substantial reductions may occur in lean tissue mass in various organs, in addition to the loss of fat stores (Battley et al. 2000).

Red Knots (*Calidris canutus*) breeding in the High Arctic regions of the northeastern Canadian High Arctic and of Greenland belong to the race *islandica*, and migrate to European wintering quarters (Salomonsen 1951, Godfrey 1953, 1992, Morrison 1984, Davidson and Wilson 1992). In the spring, most pass northwards through Iceland where they undergo the morphological changes described above during a three-week stopover (Morrison and Wilson 1992, Wilson and Morrison 1992, Piersma et al. 1999). Knots departing Iceland are thus highly adapted for flight, but on arrival in the High Arctic are unlikely to be suitably adapted for breeding, especially considering the organ reductions that take place during such flights (Battley et al. 2000). Red Knots and Ruddy Turnstones (*Arenaria interpres*) arrive at Alert with substantial stores of fat and protein remaining (Morrison and Davidson 1990). These stores could serve several purposes, including: (1) providing energy stores for survival during severe weather or food shortages in the postarrival period, and (2) providing the nutritional resources needed for successful reproduction, including physical changes in the birds themselves and egg laying. For shorebirds at Alert, studies using stable isotopes have shown that body stores are not generally used directly in egg formation,

except possibly in the earliest-laid eggs (Morrison and Hobson 2004). The same appears to hold for shorebirds in other parts of the Canadian Arctic (Klaassen et al. 2001) further suggesting that body stores are used for survival or for facilitating morphological changes before breeding. In this paper we examined morphological changes in Red Knots following arrival at Alert to address these questions.

## METHODS

### STUDY AREA

We studied body condition of Red Knots at Alert (82°30'N, 62°20'W), on the northeast coast of Ellesmere Island, Nunavut, Canada. Much of the terrain consists of frost-shattered rock, gravel, and bare clay, with very low (<15%) vegetation cover; marshy ground may occur where moisture accumulates (Brugeman and Calder 1953), but even here cover is rarely continuous.

The summer climate is severe, with mean temperatures for June, July, and August of  $-1.0^{\circ}\text{C}$ ,  $+3.4^{\circ}\text{C}$ , and  $+1.0^{\circ}\text{C}$ , respectively (1961–1990, Environment Canada 2003). These temperatures are colder than those recorded from the interior and west-central areas of Ellesmere Island owing to the cooling effects of persistent sea ice along the north and northeastern coasts (England et al. 1981). In the spring, snow cover is variable, but is usually extensive with scattered patches of open tundra, through the end of May. Temperatures generally reach the freezing point after the first week of June, and snow cover declines rapidly thereafter (Davidson and Morrison 1989).

Fieldwork involving capture and collection of specimens was carried out from 31 May to 13 June 1986, from 27 May to 10 June 1987 and from 31 May to 13 June 1990. Additional banding studies were carried out from late May to the end of June in 1999 and 2003.

### SAMPLE COLLECTION

Birds were captured by rocket net on the garbage dump and near the sewage outfall stream near Alert. Data from all years were grouped into four periods: Period 1, 28–30 May; Period 2, 31 May–2 June; Period 3, 3–5 June; and Period 4, 6–9 June. Arrivals take place chiefly between late May and 3 June (MacDonald 1953, Morrison 1992), so that data from Periods 1 and 2 refer principally to newly arrived birds. Samples from Periods 3 and 4 in early June contain mostly birds in the postarrival phase, though some newly arrived individuals may also occur.

### CONDITION ANALYSES

Following capture, birds were weighed (to nearest 1 g using a spring balance) and measured (wing chord: maximum flattened length to nearest mm; bill: exposed culmen to nearest 0.1 mm). Following collection in 1986, small samples of pectoralis muscle and liver were removed for ultrastructural studies (Evans et al. 1992). Sex was determined by gonadal inspection. Carcasses were sealed in plastic bags, frozen, and returned frozen to the laboratory.

After thawing, specimens were skinned, and the following parts dissected for separate analysis: pectoralis major and supracoracoideus muscles, liver, heart, giz-



zard, proventriculus, intestines, and gonads, plus the remaining parts consisting of other organs, skin, feathers, and skeleton. Intestinal length was measured to the nearest mm. All parts were weighed to the nearest 0.1 g and dried to constant mass at 60°C. The dried tissues were weighed to the nearest 0.1 g, packed in filter paper, and fat extracted in a Soxhlet apparatus, using petroleum ether (boiling point range 40–60°C). Body parts were again dried to constant mass and reweighed to obtain the lean (“fat-free”) dry mass. Fat loss was estimated as the loss of mass occurring during extraction.

#### STATISTICAL ANALYSES

In view of the small body size variation in the birds, mass values were not corrected for body size (van der Meer and Piersma 1994, Piersma et al. 1999). Statistical procedures were carried out using Statistica (Version 6, Statsoft, Inc. 2003). ANOVA and MANOVA were used to examine effects of sex, time period, and combinations of these on body composition measures. Independent two-tailed *t*-tests were used to compare measurements of populations. Values reported are means  $\pm$  SD.

#### RESULTS

##### ARRIVAL AND SEX RATIO

In 1986, four Red Knots were present on 31 May; numbers peaked at 43 on 3 June, and dropped steadily thereafter. In 1987, knots were first observed on 30 May; numbers increased to 35 on 5 June, and decreased rapidly thereafter. In 1990, 28 knots were present on 31 May; numbers peaked at 35 on 2 June, and decreased steadily during the next week. Many early arrivals remain and breed in the Alert area: of 95 knots captured and color-banded during late May and June in 1987–1990, 1999, and 2003, 67 (71%) were seen two days or more after banding or in subsequent years (varying from 57% in 2003 to 93% in 1999). We therefore treated the morphological patterns observed in sampled birds as reflecting those of locally breeding individuals.

Body composition analyses were carried out for 33 knots ( $n = 3, 12, 8$ , and  $10$  in Periods 1, 2, 3, and 4, respectively). Knots collected in the immediate post-arrival period (Periods 1–2) contained more males (67%) than females, while later arrivals (Periods 3–4) contained more females (67%) than males.

##### MORPHOLOGICAL MEASUREMENTS

Wing length of males collected at Alert ( $171.8 \pm 3.4$  mm,  $n = 16$ ) were similar ( $t_{41} = 1.3$ ,  $P = 0.20$ ) to those of males collected on migration in Iceland (Piersma et al. 1999;  $170.4 \pm 3.5$  mm,  $n = 27$ ); wing lengths of females in the two areas also did not differ significantly (Alert:  $174.8 \pm 5.2$  mm,  $n = 16$ ; Iceland:  $173.0 \pm 3.8$  mm,  $n = 32$ ;  $t_{46} = 1.2$ ,  $P = 0.18$ ). There were also no differences between the two areas in bill lengths of males (Alert:  $32.1 \pm 1.9$  mm,  $n = 16$ ; Iceland:  $32.2 \pm 1.4$  mm,  $n = 7$ ;  $t_{21} = 0.3$ ,  $P = 0.74$ ) or of females (Alert:  $33.3 \pm 1.8$  mm,  $n = 17$ ; Iceland:  $33.8 \pm 1.5$  mm,  $n = 32$ ;  $t_{47} = 1.0$ ,  $P = 0.30$ ). These results are consistent with the idea that the birds belong to the same population (Davidson and Wilson 1992).

At Alert, wing and bill measurements did not differ between years (1986 and 1987) for males and females (males: wing,  $F_{1,14} = 0.2$ ,  $P = 0.66$ ; bill,  $F_{1,14} = 0.001$ ,  $P = 0.97$ ; females: wing,  $F_{1,14} = 4.6$ ,  $P = 0.05$ ; bill,  $F_{1,14} = 2.7$ ,  $P = 0.12$ ), therefore we combined data from the two years (and the one bird from 1990). There were no significant differences between any of these measurements within each sex over the four periods following arrival (males: wing,  $F_{3,12} = 0.8$ ,  $P = 0.24$ ; bill,  $F_{3,12} = 0.4$ ,  $P = 0.75$ ; females: wing,  $F_{3,12} = 1.6$ ,  $P = 0.24$ ; bill,  $F_{3,12} = 1.3$ ,  $P = 0.33$ ), so that differences in other body components are not likely to have arisen from structural differences in size of the birds.

##### CHANGES IN BODY MASS

Mean mass of knots in each arrival period were very similar among years ( $n = 153$  birds between 1974 and 2003, Fig. 1): mean masses of birds did not differ across years in Period 1 ( $F_{1,4} = 0.5$ ,  $P = 0.53$ ), Period 2 ( $F_{4,28} = 1.0$ ,  $P = 0.45$ ), or Period 4 ( $F_{4,18} = 0.4$ ,  $P = 0.81$ ). The significant variation across years in Period 3 ( $F_{7,63} = 2.4$ ,  $P = 0.03$ ) may have resulted from low masses in 1976 and 1999 compared to the long-term mean (Fig. 1); after removal of data from these years, there were no significant differences across years ( $F_{5,53} = 0.8$ ,  $P = 0.54$ ). Thus, we conclude that 1986, 1987, and 1990 were typical years in terms of mass changes after arrival on the breeding grounds.

After arrival, male and female Red Knots both lost overall body mass (Fig. 2). There were significant differences across sexes and periods (MANOVA: sex,  $F_{1,28} = 9.9$ ,  $P < 0.01$ ; period,  $F_{3,28} = 5.0$ ,  $P < 0.01$ ). Fat mass decreased significantly throughout the postarrival period for both males ( $F_{3,12} = 5.0$ ,  $P = 0.02$ ) and females ( $F_{3,13} = 8.1$ ,  $P < 0.01$ ); there was no significant difference in fat content between the sexes ( $F_{1,31} = 0.9$ ,  $P = 0.34$ ). Total lean dry mass remained fairly constant over the postarrival period for both sexes, but was lower for males collected in Period 4 ( $F_{3,12} = 4.7$ ,  $P = 0.02$ ). Overall, total lean dry mass of females ( $42.9 \pm 3.2$  g,  $n = 17$ ) was significantly greater than that of males ( $38.8 \pm 2.8$  g,  $n = 16$ ;  $F_{1,31} = 15.6$ ,  $P < 0.01$ ).

##### ORGAN CHANGES

**Nutritional organs.** Three parts of the digestive system all showed similar patterns of increase during the post-arrival period (Fig. 3). Gizzard lean dry mass did not differ between the sexes ( $F_{1,31} = 0.9$ ,  $P = 0.34$ ), and increased significantly across periods for both sexes (males:  $F_{3,25} = 5.0$ ,  $P = 0.02$ ; females:  $F_{3,13} = 8.1$ ,  $P < 0.01$ ). Lean dry mass of the proventriculus was significantly higher in females than males ( $F_{1,20} = 10.2$ ,  $P < 0.01$ ). When the sexes were considered separately, there was no change in proventriculus lean dry mass among time periods (males:  $F_{1,6} = 0.8$ ,  $P = 0.55$ ; females:  $F_{2,9} = 2.7$ ,  $P = 0.12$ ); however, periods 1 and 3 were significantly different from each other ( $F_{1,9} = 8.6$ ,  $P = 0.02$ ) when sexes were combined, showing an increase in mass after arrival. Overall mean gut length of males was significantly shorter than that of females ( $F_{1,21} = 5.74$ ,  $P = 0.03$ ) and there was an increasing pattern over the postarrival period, similar to the other digestive organs, but which was not sta-

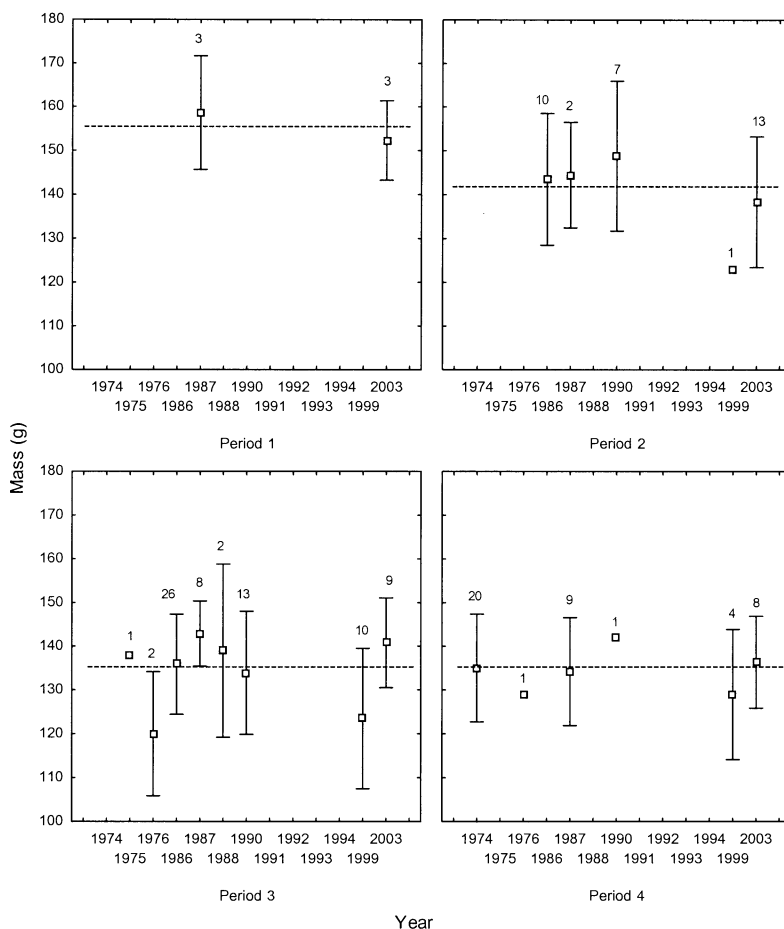


FIGURE 1. Mean masses of Red Knots captured or collected at Alert during post-arrival periods spanning 28 May–9 June 1974–2003. Period 1 = 28–30 May, Period 2 = 31 May–2 June, Period 3 = 3–5 June, and Period 4 = 6–9 June. Unfilled squares and whiskers indicate mean  $\pm$  SD and sample sizes are shown above the whiskers. Dashed lines indicate the overall means for each respective period.

tistically significant (males:  $F_{3,6} = 1.3$ ,  $P = 0.35$ ; females:  $F_{2,10} = 0.3$ ,  $P = 0.72$ ).

Mean dry liver mass of males and females did not differ ( $F_{1,21} = 2.8$ ,  $P = 0.11$ ) so we pooled data for both sexes. Both sexes showed mass increases after arrival ( $F_{3,19} = 3.1$ ,  $P = 0.05$ ), birds collected in later periods (Periods 3 and 4) having significantly heavier dry liver mass ( $F_{1,21} = 5.2$ ,  $P = 0.03$ ) than birds collected earlier in the season (Periods 1 and 2).

**Exercise organs.** During the post arrival period, lean dry pectoral muscle mass was significantly lower in males than females and tended to decrease across periods (Fig. 4, MANOVA: sexes:  $F_{1,25} = 4.8$ ,  $P = 0.04$ ; periods:  $F_{3,25} = 2.6$ ,  $P = 0.08$ ), with a significant decrease between periods 1 and 4 (sex:  $F_{1,9} = 12.5$ ,  $P < 0.01$ ; period:  $F_{1,9} = 21.7$ ,  $P < 0.01$ ). Pectoral muscle mass and fat mass were significantly correlated (males:  $r = 0.70$ ,  $P < 0.01$ ; females:  $r = 0.53$ ,  $P = 0.03$ ; both sexes:  $r = 0.54$ ,  $P < 0.01$ ). Heart lean dry mass of males and females did not differ ( $F_{1,21} = 0.8$ ,  $P =$

0.40); both increased, by factors of 2 and 2.7 times, respectively, between periods 1 and 4. Heart lean dry mass was significantly higher during Period 3 compared to the immediate postarrival period (Period 1,  $F_{1,9} = 8.1$ ,  $P = 0.02$ ). Lean dry mass of the remaining body components was, on average, lower in males than females ( $F_{1,31} = 17.0$ ,  $P < 0.01$ ) and for males there were significant changes among time periods ( $F_{3,12} = 5.0$ ,  $P = 0.02$ ).

**Gonads.** Male testis size showed little change during the postarrival period ( $F_{3,12} = 0.3$ ,  $P = 0.82$ ), with largest testis averaging  $11.3 \pm 2.5$  mm ( $n = 16$ ). Testis size ranged from 3.9–14.9 mm, with 13 of the 16 measurements falling between 10–15 mm, indicating that gonads were well developed (Nettleship 1974). Mean size of the largest ovum in females increased from  $4.5 \pm 1.2$  mm ( $n = 4$ ) in Period 2 to  $7.6 \pm 4.4$  mm ( $n = 6$ ) in Period 4, but differences across periods were not significant ( $F_{3,13} = 0.9$ ,  $P = 0.47$ ).

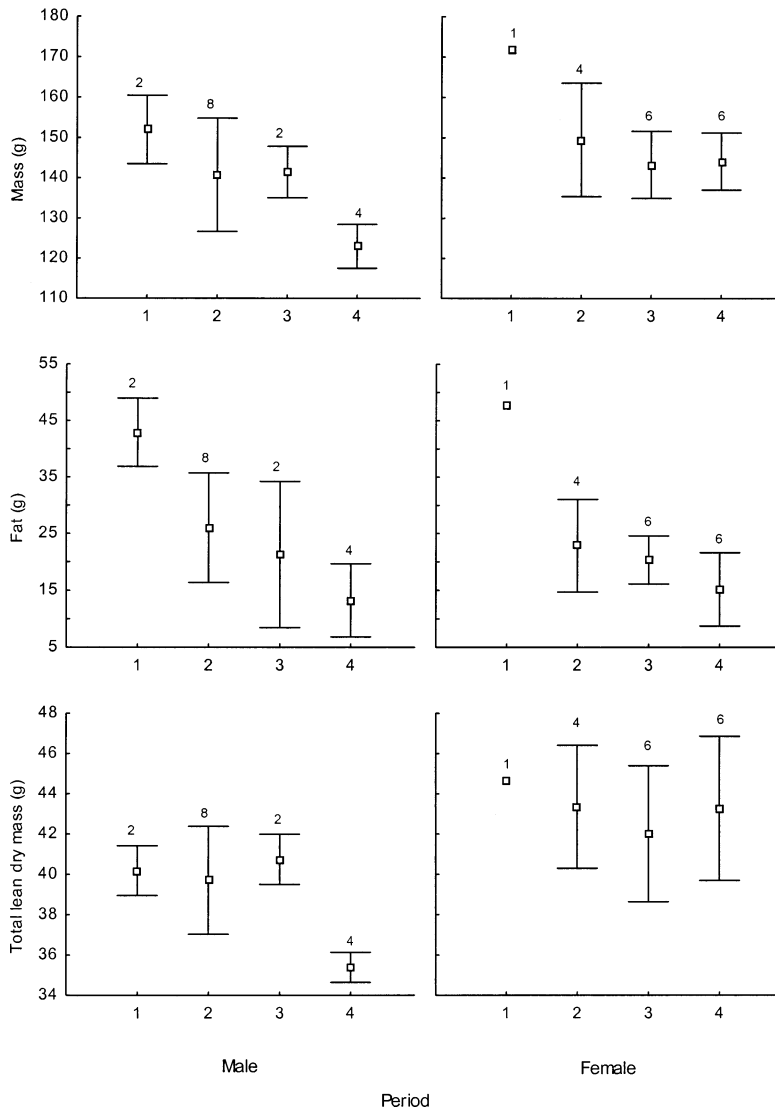


FIGURE 2. Changes in total body composition (mass, fat mass, lean dry mass) of male and female Red Knots after arrival at Alert. See Figure 1 for dates of each time period. Unfilled squares and whiskers indicate mean  $\pm$  SD and sample sizes are shown above the boxes.

## DISCUSSION

We found many morphological changes in Red Knots after arrival at Alert. The earliest arrivals carried substantial stores of fat and protein; overall mass and fat content exceeded those of birds arriving on spring migration in Iceland (Piersma et al. 1999) and Norway (Davidson and Evans 1986), and of knots at the beginning and end of the wintering period in the United Kingdom (Morrison 1977). Pectoral muscle stores were similar to those on arrival in Iceland (Piersma et al. 1999), somewhat larger than those on spring migration in northern Norway, and clearly larger than

those of knots wintering in the United Kingdom (Davidson and Evans 1986, 1989).

Fat and protein stores were both lost rapidly after arrival at Alert. The consistent pattern of mass loss after arrival in different years suggests the changes are part of a pattern that occurs every year. Knots in captivity are known to have strong circannual rhythms in mass changes and basal metabolic rate similar to those of wild birds (Piersma et al. 1995, Cadée et al. 1996, Piersma 2002). Changes in pectoral muscle size are not dependent on power training, but are likely under the control of an endogenous circannual process: they tend

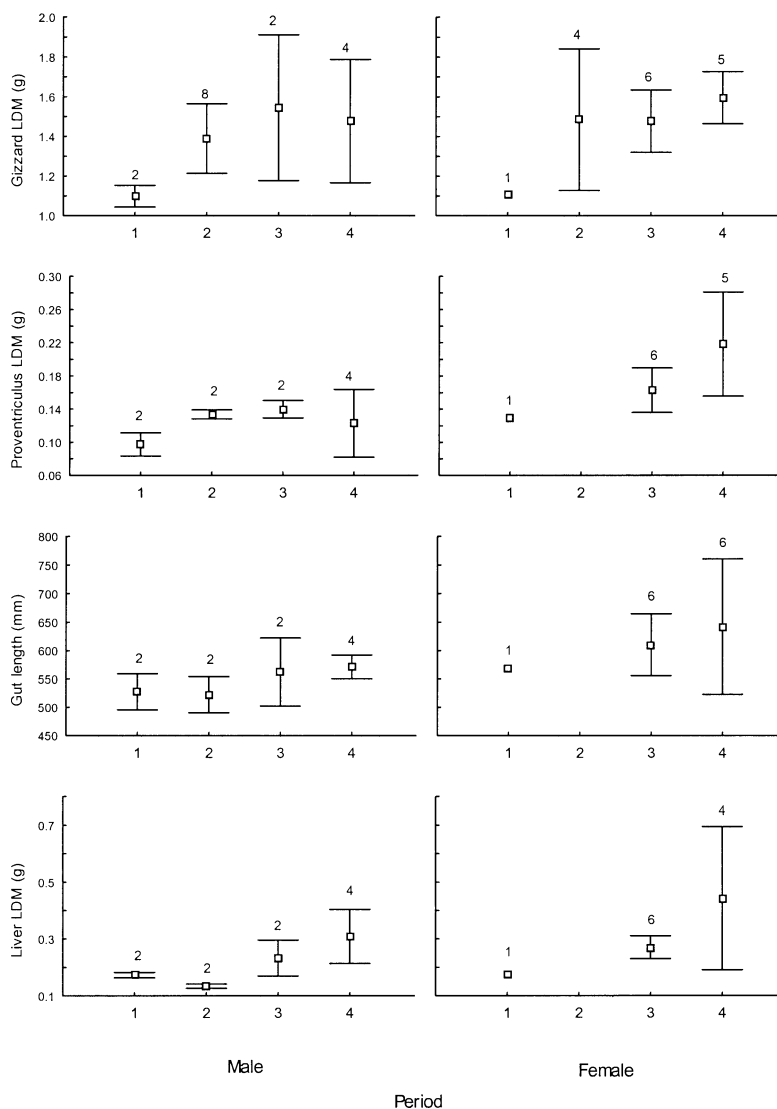


FIGURE 3. Changes in “nutritional organs” (gizzard lean dry mass [LDM], proventriculus LDM, gut length, and liver LDM) of male and female Red Knots after arrival at Alert. See Figure 1 for dates of each time period. Unfilled squares and whiskers indicate mean  $\pm$  SD and sample sizes are shown above the boxes.

to occur in parallel with changes in body mass (Dietz et al. 1999, Lindström et al. 2000).

Bringing endogenous stores to the breeding grounds presumably provides the birds with adaptive advantages that outweigh the cost of transporting such stores to the Arctic. Endogenous stores may provide nutritional resources for breeding, including egg formation: birds relying on endogenous stores have been termed “capital breeders,” while those relying on local food resources are referred to as “income breeders” (Drent and Daan 1980, Bonnet et al. 1998, Meijer and Drent 1999). Studies using stable isotopes have now shown that most Arctic-nesting shorebirds do not adopt a cap-

ital strategy but instead rely mostly on local food resources for egg formation (Klaassen et al. 2001, Morrison and Hobson 2004). At Alert, egg components reflected a local, terrestrial source of nutrients, with little indication of any contribution from body stores accumulated in marine habitats during migration or on wintering grounds (Morrison and Hobson 2004); eggs in some of the earliest-laid clutches, however, showed possible input of nutrients from marine sources. The rapid decline in fat and protein stores after arrival at Alert suggests that stored nutrients would not be available by the time most clutches are laid, even allowing for follicular development, which requires 5–6 days

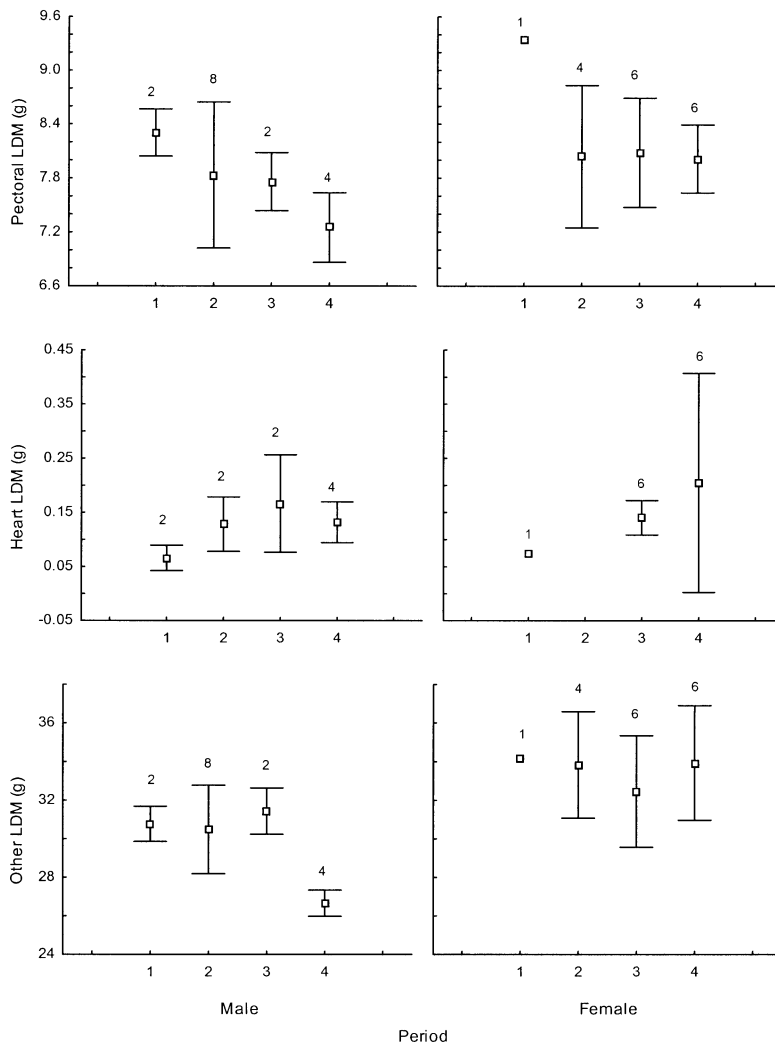


FIGURE 4. Changes in lean dry mass (LDM) of “exercise organs” (pectoral muscles, heart, and other body components) of male and female Red Knots after arrival at Alert. See Figure 1 for dates of each time period. Unfilled squares and whiskers indicate mean  $\pm$  SD and sample sizes are shown above the boxes.

before laying (Roudybush et al. 1979): the mean estimated clutch completion date for 19 Red Knot nests from 1974–1976 and 1986–1991 on northern Ellesmere Island was 20 June  $\pm$  7 days (range 8–30 June, RIGM, unpubl. data). For clutches completed as early as 8 June, however, it is possible that some residual stores could be used for egg formation.

Fat and protein stores could provide energy or nutrients after arrival in years when the weather may be poor, or food resources are limited or unavailable. Birds leaving Iceland in better than average condition are more likely to survive severe summers (RIGM, NCD, and J. R. Wilson, unpubl. results); on the breeding grounds, starvation can occur during periods of prolonged bad weather (Morrison 1975). Knots of the *rufa* subspecies have been shown to experience reduced survival in

years when they were unable to acquire adequate stores at the final stopover site during spring migration (Baker et al. 2004). In 1999, postarrival masses of knots at Alert were lower than the long-term mean, and many shorebirds were unable to breed, or bred late, owing to extensive early season snow cover. The need to use stores for survival or supplementing lower-than-usual local food resources in that year may have contributed to delayed or failed breeding.

Another important function of body stores may be to provide the energy and nutrients needed for restoration of various tissues after losses during migration (Battley et al. 2000). Although knots leave their final staging grounds in Iceland well adapted for migration, their arrival condition at Alert is unlikely to be well adapted for successful breeding. After arrival, knots may need



to go through a "recovery" period in which they rebuild the organs that have been reduced prior to, or during, flight and which are needed for reproductive activities. Stores of fat and protein brought to the breeding grounds may enable these processes to start at a time when few feeding opportunities are available. Given the well-documented advantages that Arctic-breeding birds may acquire through nesting as early as possible, and the need to fit all phases of reproduction into the short season, the ability to arrive on the breeding grounds with stores of fat and protein may be an important aspect of shorebirds' ability to nest successfully in the High Arctic. The suite of morphological changes that takes place after arrival, including increases in heart, liver, gizzard, proventriculus, intestines, and possibly gonads, occurs at the same time as fat and protein stores are being lost. It therefore seems likely, if not inevitable, that metabolites from fat and protein stores will be used to enable these other body changes to take place. Stores acquired at staging areas remote from the nesting grounds may thus play a key role in enabling shorebirds to breed successfully in the Arctic.

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## LIPID RESERVES OF MIGRANT SHOREBIRDS DURING SPRING IN PLAYAS OF THE SOUTHERN GREAT PLAINS

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**Abstract.** Inland-migrating shorebirds rely on wetlands as stopover sites to replenish nutrient reserves.

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Because wetlands are spatially and temporally dynamic, shorebirds may accumulate highly variable lipid reserves. We compared lipid reserves among four shorebird species (American Avocets [*Recurvirostra americana*], Long-billed Dowitchers [*Limnodromus scolopaceus*], Least Sandpipers [*Calidris minutilla*], and Western Sandpipers [*C. mauri*]) collected from playa wetlands in the southern Great Plains during spring 1993 and 1994. Because playas are ephemeral, we had

the opportunity to examine the influence of a variable environment (a wet year and a dry year) on lipid reserves. Additionally, we examined the influence of different migration distances and strategies, and body sizes on lipid reserves. Western Sandpipers had the highest lipid reserves (41%–50%) and Dowitchers had the lowest reserves (18%). Least and Western Sandpipers had 7%–9% higher lipid reserves in the wet year than dry year. Thus, small-bodied shorebirds may be more affected by variable habitat conditions than large-bodied shorebirds because of their higher mass-specific metabolic rates.

**Key words:** *American Avocet, Least Sandpiper, lipid reserves, Long-billed Dowitcher, shorebirds, Western Sandpiper.*

### Reservas Lipídicas de Aves Playeras Migrantes Durante la Primavera en Humedales del Sur de la Gran Planicie

**Resumen.** Las aves playeras que migran tierra adentro necesitan de humedales como lugares de escala migratoria para recuperar sus reservas de nutrientes. Debido a que los humedales son espacial y temporalmente dinámicos, las aves playeras pueden acumular lípidos como reserva de forma muy variable. En este estudio comparamos las reservas lipídicas entre cuatro especies de aves playeras (*Recurvirostra americana*, *Limnodromus scolopaceus*, *Calidris minutilla* y *C. mauri*) colectadas en los humedales “playa” de la parte sur de la gran planicie durante la primavera de 1993 y 1994. Debido a que estos humedales son ambientes efímeros, tuvimos la oportunidad de examinar la influencia de un ambiente variable (un año húmedo y un año seco) sobre las reservas lipídicas de las aves. Además, examinamos la influencia de distintas distancias y estrategias de migración y del tamaño corporal sobre las reservas. La especie con las mayores reservas lipídicas fue *C. mauri* (41%–50%) y la especie con las menores reservas fue *L. scolopaceus* (18%). Las dos especies de *Calidris* presentaron reservas lipídicas un 7%–9% mayores en el año húmedo que en el año seco. Por tanto, las aves playeras de tamaño pequeño podrían verse más afectadas por condiciones ambientales variables que las de tamaño grande como consecuencia de sus mayores tasas metabólicas con respecto al peso.

Shorebirds migrating through the interior of North America use wetlands along their migratory route as stopover sites to replenish lipid reserves (Skagen and Knopf 1994, Farmer and Parent 1997, Davis and Smith 1998a, DeLeon and Smith 1999). These lipid reserves are critical for shorebirds to continue migration, as well as essential for successful reproduction upon arrival on the breeding grounds (Blem 1990). Unlike coastal-migrating shorebirds that typically rely on traditional staging areas (e.g., Chesapeake Bay, Bay of Fundy) that contain predictable and abundant food resources for refueling (Myers et al. 1987), inland-migrating shorebirds rely on a variety of stopover sites that contain highly variable and unpredictable food resources (Farmer and Parent 1997, Davis and Smith

1998b). Because of their ephemeral nature (i.e., unpredictable drying and flooding cycles), these stopover sites are spatially and temporally dynamic (Fredrickson and Reid 1990, Skagen and Knopf 1993, Farmer and Parent 1997, Smith 2003). Consequently, inland-migrating shorebirds must deal with the constraints of environmental uncertainty at stopover sites, and also with constraints of a narrow window of time to arrive on their northern breeding grounds (Lindström 2002, Drent et al. 2003). These constraints play a key role in lipid-reserve deposition and use at stopover sites. For example, shorebirds may increase their lipid reserves at stopover sites as a hedge against environmental uncertainty during migration (Gudmundsson et al. 1991). Conversely, shorebirds may maintain only enough lipid reserves to continue their rapid migration northward because they are more focused on arriving on the breeding grounds early than depositing excess lipid reserves (Farmer and Wiens 1999, Battley et al. 2004).

Shorebird migration patterns are influenced by geography and food availability (Morrison 1984). In particular, migration patterns of inland-migrating shorebirds may be profoundly influenced by the distribution and availability of stopover sites as well as the distance between those sites (Farmer and Parent 1997, Farmer and Wiens 1999). O'Reilly and Wingfield (1995) noted that variation in geography and food availability leads to variation in length of flights between stopover sites. In response to this variability, shorebirds may adopt a hop (short-distance flight between stopover sites), skip (intermediate-distance flight between stopover sites), or jump (long-distance flight between stopover sites) migration strategy (Piersma 1987, O'Reilly and Wingfield 1995). Consequently, the migration strategy adopted by a shorebird species may also play a role in the amount of lipids the birds accumulate at stopover sites. For example, shorebirds that adopt a hop strategy might be expected to accumulate relatively smaller amounts of lipids than shorebirds that adopt a jump strategy.

Playa wetlands in the southern Great Plains serve as important stopover sites for migrant shorebirds (Davis and Smith 1998a, 1998b). The occurrence of playas on the landscape is variable because of their unpredictable and rapidly changing hydroperiod (e.g., several wet-dry cycles throughout the year; Smith 2003). Indeed, the availability of wetland habitat in the southern Great Plains may range from as low as 5% during dry years to as high as 80% during wet years (Smith 2003). In this landscape context, shorebirds may accumulate different amounts of lipid reserves depending on the availability of wetlands. Farmer and Wiens (1999) reported that in wet springs female Pectoral Sandpipers (*Calidris melanotos*) had larger lipid reserves than in dry springs. However, migrant shorebirds may also respond to the dry springs by having larger lipid reserves as a cushion against the uncertainty of favorable habitat conditions occurring farther north.

Here, we assess the influence of a variable environment on accumulation of lipid reserves at playa stopover sites and examine the role that different migration distances and strategies may play in lipid accumulation. We compared lipid levels among four species of

shorebirds (American Avocets [*Recurvirostra americana*], Long-billed Dowitchers [*Limnodromus scolopaceus*], Least Sandpipers [*Calidrus minutilla*], and Western Sandpipers [*C. mauri*]) using playas as stopover sites during two springs with different precipitation levels. These four species range in the distance of their migration to their breeding grounds; thus, we hypothesize that long-distance migrants (arctic-breeding shorebirds) would accumulate larger lipid reserves than short-distance migrants (American Avocets), but that long-distance and short-distance migrants could also accumulate similar amounts of lipid reserves if they adopted similar migration strategies (e.g., hop strategy).

## METHODS

We conducted this study in the Playa Lakes region of the southern Great Plains in western Texas during spring of 1993 and 1994. A detailed description of the region is provided by Smith (2003). We estimated precipitation for our study area by averaging precipitation data from three weather stations within the region (Hereford, Texas; Lubbock, Texas; and Lamesa, Texas; National Oceanic and Atmospheric Administration 2004). We selected these weather stations because they are located in the northern, middle, and southern portions of the study area. We calculated total annual precipitation levels (January–December) for 1992 and 1993 and premigration precipitation levels (September–March 1992–1993 and 1993–1994) because precipitation during that period should affect availability of playas during spring migration.

We randomly collected actively foraging American Avocets, Long-billed Dowitchers, Least Sandpipers, and Western Sandpipers from 31 playas (18 in 1993, 13 in 1994) in Castro, Dawson, Floyd, Howard, Lynn, Martin, and Parmer Counties in western Texas (an area located between 32°30'N and 34°41'N and 101°09'W and 102°30'W) during spring migration (10 March–28 May 1993, 27 February–23 May 1994, Davis and Smith 1998b). To obtain a representative sample of each species throughout their migration in the Playa Lakes region, we collected each species from the early, middle, and late periods of their migration. Because migration chronologies of these species vary considerably (4–8 weeks, Davis and Smith 1998b), we collected some species over a longer period than others (Table 1). We could not determine age for each shorebird, but determined gender by internal examination. Birds were placed in plastic bags and stored frozen until analyzed.

In the laboratory, we removed gastrointestinal tract contents from thawed birds, dried them with paper towels to remove excess moisture, and weighed them to the nearest 0.1 g to determine wet body mass. Birds were then refrozen. Because of their larger size, we sectioned frozen carcasses of American Avocet and Long-billed Dowitcher with a meat saw before freeze-drying the sectioned carcasses to constant mass. For Least and Western Sandpipers, we freeze-dried their unsectioned carcasses to constant mass. Dried sections of each American Avocet and Long-billed Dowitcher and the dried carcass of each Least and Western Sandpiper were then ground in a commercial blender to

homogenize each sample. Percent lipid was determined by extraction from duplicate 5–10 g samples of dried homogenate using diethyl ether in a Soxhlet apparatus for 40 hr (Dobush et al. 1985).

## STATISTICAL ANALYSES

We used a three-way analysis of covariance with days post initial collection as a covariate to examine differences in percent fat among the four species and between sexes and years (SYSTAT 1992). Percent fat was the dependent factor and species, sex, and year were independent factors. For this analysis, days post initial collection was calculated as the interval between the date when an individual bird was collected and the date when the first bird of that species was collected. We used days post initial collection as a covariate because nutrient reserves within a species might vary by arrival date during spring migration (i.e., birds collected later at the stopover site may have greater fat reserves than birds collected earlier at the stopover site, Lyons and Haig 1995). Prior to statistical analysis, data were also tested for normality and equal variances. Fisher's least significant difference test was used to examine differences among species. To reduce the likelihood of making a Type II error, statistical tests were considered significant at  $P \leq 0.10$ . Values are presented as means  $\pm$  SE.

## RESULTS

### PRECIPITATION

Normal annual precipitation (average over 50 years, 1947–1997) for the region was  $45.7 \pm 1.8$  cm. In 1992 precipitation was 38% above the 50-year average (60.9 cm), while in 1993 precipitation was 28% below average (38.4 cm). Moreover, premigration precipitation for 1992–1993 was close to normal (1.2 cm below 50-year average for this time period), while in 1993–1994 it was below normal (10.2 cm below 50-year average). Hereafter, we refer to 1992–1993 as the wet year and 1993–1994 as the dry year.

### PERCENT FAT

There was no three-way interaction ( $F_{3,195} = 1.4$ ,  $P = 0.23$ ), but there was a significant species  $\times$  year interaction ( $F_{3,195} = 5.6$ ,  $P = 0.001$ ) and a sex  $\times$  year interaction ( $F_{1,195} = 4.0$ ,  $P = 0.05$ ). Days post initial collection for percent fat was not significant ( $F_{1,195} = 1.0$ ,  $P = 0.33$ ). Therefore, subsequent analyses examined percent fat among species within each year, and for each species between years. In 1993, there was a significant difference in the percent fat among species ( $F_{3,110} = 38.8$ ,  $P < 0.001$ ), but not between sexes ( $F_{1,110} = 1.3$ ,  $P = 0.25$ ). There was no species  $\times$  sex interaction ( $F_{3,110} = 1.2$ ,  $P = 0.30$ ). Percent fat was highest in Western Sandpipers and lowest in Long-billed Dowitchers during 1993 (Table 1). In 1994, percent fat also differed among species ( $F_{3,86} = 22.7$ ,  $P < 0.001$ ), but not between sexes ( $F_{1,86} = 2.2$ ,  $P = 0.15$ ). There was no species  $\times$  sex interaction ( $F_{3,86} = 1.4$ ,  $P = 0.25$ ). In 1994, Western Sandpipers had the highest percent fat, while Long-billed Dowitchers had the lowest (Table 1). For Avocets, percent fat was higher in the dry year than the wet year ( $F_{1,57} = 6.6$ ,  $P = 0.01$ ), whereas percent fat was higher in the wet year than the dry



TABLE 1. Collection dates and percent fat of American Avocets, Long-billed Dowitchers, Least Sandpipers, and Western Sandpipers collected during spring from playa wetlands on the Southern High Plains of Texas, 1993–1994. Values are presented as mean  $\pm$  SE with ranges in parentheses. Mean percent fat among species in each year were significantly different from one another (all  $P < 0.10$ ).

Species	1993			1994		
	$n^a$	Collection date (days)	Percent fat	$n$	Collection date (days)	Percent fat
American Avocet	8 M, 9 F	22 Apr $\pm$ 3.2 (2 Apr–8 May)	27.0 $\pm$ 2.5 (12.2–54.6)	14 M, 28 F	16 Apr $\pm$ 2.0 (1 Apr–8 May)	34.9 $\pm$ 1.7 (10.7–56.9)
Long-billed Dowitcher	21 M, 24 F	20 Mar $\pm$ 1.1 (6 Mar–3 Apr)	18.3 $\pm$ 1.0 (3.9–31.1)	23 M, 12 F	13 Mar $\pm$ 1.4 (27 Feb–25 Mar)	18.5 $\pm$ 0.9 (8.9–34.8)
Least Sandpiper	29 M, 20 F	21 Apr $\pm$ 1.6 (2 Apr–5 May)	33.3 $\pm$ 1.5 (14.5–49.4)	6 M, 6 F	5 Apr $\pm$ 4.0 (14 Mar–16 Apr)	26.8 $\pm$ 1.2 (21.1–34.7)
Western Sandpiper	3 M, 6 F	21 Apr $\pm$ 1.6 (14–27 Apr)	49.9 $\pm$ 2.5 (39.3–60.5)	3 M, 7 F	19 Apr $\pm$ 2.7 (9–26 Apr)	40.9 $\pm$ 3.4 (15.7–51.5)

<sup>a</sup> M = males, F = females.

year for Least ( $F_{1,59} = 4.6$ ,  $P = 0.04$ ) and Western Sandpipers ( $F_{1,17} = 4.3$ ,  $P = 0.05$ , Table 1). Percent fat for Long-billed Dowitchers was similar between years ( $F_{1,78} = 0.01$ ,  $P = 0.92$ ).

## DISCUSSION

We compared lipid levels of three arctic-breeding shorebirds and one temperate breeder. Interestingly, we observed only one of the arctic-breeding species (Western Sandpipers) having larger lipid levels than American Avocets, the temperate breeder. It is probable that some avocets were close to or on their breeding grounds; Conway et al. (2005) reported that avocets commonly nest in the Playa Lakes Region. Hence, higher lipid reserves in avocets may be due to the birds rapidly depositing lipids for breeding. We observed a large disparity in lipid levels among the arctic-breeding shorebirds, with Western Sandpipers having the highest reserves (41%–50%), Least Sandpipers having moderate levels (27%–33%), and Long-billed Dowitchers having the lowest (18%). We also compared lipid levels between wet and dry years and found that Least and Western Sandpiper lipid levels were 7%–9% higher in wet years than dry years, and American Avocet lipid levels were 8% higher in dry years than wet years. Variation in our results suggests that several intrinsic and extrinsic factors, acting separately or jointly, play roles in accumulation of lipid reserves by migrant shorebirds at stopover sites.

Of the three arctic breeders, Long-billed Dowitchers migrate the farthest distance (8000–10 000 km [Takekawa and Warnock 2000] vs. 5000–8000 km for Western and Least Sandpipers [Cooper 1994, Wilson 1994]) from the Playa Lakes Region to their breeding grounds. Owing to the longer migration distance, Long-billed Dowitchers would be expected to accumulate similar, if not higher, lipid levels than both Western and Least Sandpipers. Consequently, the disparity in lipids between Long-billed Dowitchers, Least Sandpipers, and Western Sandpipers is surprising. Because we collected a random, representative sample of each species throughout their migration in the Playa Lakes Region, we believe it is unlikely that this dis-

parity in lipid levels is due to inadequate sampling (i.e., only collecting early or late migrants). However, our findings could have been influenced by small sample sizes, especially for Western Sandpipers.

Differences in lipid levels may also be a function of species adopting different migration strategies. For example, Long-billed Dowitchers generally have shorter migration bouts than most other Nearctic-breeding shorebirds (Takekawa and Warnock 2000) which may explain their relatively low lipid reserves. Conversely, Western Sandpipers may accumulate large lipid reserves to fuel longer migration bouts. Alternatively, Western Sandpipers and Long-billed Dowitchers may adopt different time-energy strategies. For Western Sandpipers, high lipid levels may be explained by the birds adopting an energy-maximization strategy (Farmer and Wiens 1999) of maintaining high lipid reserves as a hedge against a less hospitable and unpredictable environment at stopover sites farther north (O'Reilly and Wingfield 2003). For Long-billed Dowitchers, a time-minimization strategy could explain their low lipid levels; they may forgo advantages of high lipid levels for the advantage of arriving on the breeding grounds as early as possible to secure preferred breeding sites (Lindström and Ålerstam 1992, Farmer and Wiens 1999). Body size differences between Long-billed Dowitchers and Least and Western Sandpipers also may contribute to the disparity in lipid reserves. Small-bodied shorebirds have higher mass-specific metabolic rates than large-bodied shorebirds (Calder 1974, Pienkowski and Evans 1984, Lindström and Klaassen 2003).

Differences in prey abundances and weather conditions during migration also may influence lipid levels. Invertebrate abundances were lower in early migration (0.1 g m<sup>-2</sup>, late February–mid-March) than late migration (1.0 g m<sup>-2</sup>, early April–early May, Davis 1996). Low temperatures (<0°C) and strong winds (>33 km hr<sup>-1</sup>) were also more common in early migration (Davis 1996). Low lipid levels in Long-billed Dowitchers, the earliest migrant (late February and early March; Davis 1996), may be partially explained by reduced prey abundances and increased thermoregulatory costs associated with the timing of their migration. In contrast to dow-



itchers, most individuals of the other species migrated through the region from early to late April (Davis and Smith 1998b). Therefore, these species likely benefited from higher prey abundances and more favorable weather during the latter part of the migration by being able to maintain and possibly increase lipid reserves during migration through the Playa Lakes Region.

Given the ephemeral nature of playas, it is not surprising that lipid levels were variable. When these species use a playa, they likely cannot discriminate between profitable and unprofitable prey (Davis and Smith 2001). Instead, they adopt an opportunistic foraging strategy of selecting the most abundant prey regardless of its nutritional or energetic quality (Davis and Smith 2001). Moreover, prey abundances among playas are variable. For example, prey abundances in our study playas ranged from 0.02 g m<sup>-1</sup> to 4.5 g m<sup>-1</sup> (Davis 1996). Depending on the quality and quantity of prey items in a playa, shorebirds may or may not be able to buildup lipids during their stay at a playa.

Farmer and Wiens (1999) found that female Pectoral Sandpipers accumulated higher lipid reserves than males during spring and hypothesized these differences were due to each sex employing a different strategy to accumulate reserves at stopover sites. Females may use a strategy to increase lipid reserves as they migrate north to enhance reproductive success, and males may use a strategy to maintain just enough lipid reserves to allow them to arrive on the breeding grounds first to secure territories. Although each of our study species has a similar mating system (i.e., monogamous, territorial, and shared incubation duties [Cooper 1994, Wilson 1994, Robinson et al. 1997, Takekawa and Warnock 2000]), Least and Western Sandpipers are the only species in which the males arrive on breeding grounds prior to females (Cooper 1994, Wilson 1994). However, we observed no differences in lipid reserves between sexes though low sample sizes may have reduced the power to detect differences.

Above-normal precipitation resulted in playas being more abundant and widespread in 1993 than 1994. Least and Western Sandpipers appeared to be influenced by habitat conditions during the wet year because their lipid reserves were larger during that year. They were probably able to accumulate relatively higher lipid reserves because they avoided flying longer distances in search of suitable stopover sites during the wet year (Farmer and Wiens 1999). Dowitchers and avocets appeared to be unaffected by the interannual variation in habitat conditions. Although it is difficult to explain interannual patterns in lipid reserves for dowitchers and avocets, large-bodied shorebirds may not be as affected by lower-quality habitat conditions as small-bodied shorebirds because they have lower mass-specific metabolic rates (Calder 1974, Pienkowski and Evans 1984, Lindström and Klaassen 2003) and can feed on a wider variety of prey (Davis and Smith 1998b).

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## THE EFFECT OF THE 1997–1998 EL NIÑO ON RHINOCEROS AUKLETS ON PROTECTION ISLAND, WASHINGTON

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**Abstract.** The 1997–1998 El Niño event was one of the most severe warm episodes the Pacific Ocean

experienced during the 20th century. In Washington, it resulted in above-normal sea surface temperatures and sea levels during 1997–1998 on the state's outer coast and in the Strait of Juan de Fuca. Sea surface temperature anomalies of the two areas were highly correlated during 1995–2000. Rhinoceros Auklet (*Cerorhinca monocerata*) chick growth rates on Protection Island

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in the eastern Strait of Juan de Fuca were significantly lower (19%) during the El Niño years. Although chicks' peak weights were lowest during 1997, they did not significantly differ from non-El Niño years, suggesting that birds were able to compensate for smaller or less frequent chick feedings by extending the chicks' time in the burrow. Consequently, chicks were also significantly older at peak weight during this warm event, which likely led to prolonged fledging periods. However, the 1997–1998 El Niño did not affect other aspects of Rhinoceros Auklets reproductive behavior: chick mortality, although highest in 1997, was not significantly different among years; the number of breeding attempts were similar among years; as was the timing of breeding. Thus, because of its unique breeding biology, the Rhinoceros Auklet is well adapted to ocean climatic fluctuations.

**Key words:** *Cerorhinca monocerata*, *El Niño*, growth rate, *Rhinoceros Auklet*, sea level, sea surface temperature, Washington.

#### Efecto de El Niño de 1997–1998 en *Cerorhinca monocerata* en Protection Island, Washington

**Resumen.** El evento de El Niño de 1997–1998 fue uno de los episodios cálidos más severos que experimentó el Océano Pacífico durante el siglo XX. En Washington, esto condujo a un incremento por sobre lo normal de las temperaturas superficiales y de los niveles del mar durante 1997–1998 en la costa externa del estado y en el estrecho de Juan de Fuca. Las anomalías de la temperatura superficial del mar de las dos áreas estuvieron altamente correlacionadas durante 1995–2000. Las tasas de crecimiento de los pichones de *Cerorhinca monocerata* en Protection Island en el este del Estrecho de Juan de Fuca fueron significativamente menores (19%) durante los años de El Niño. Aunque los pesos máximos de los pichones fueron menores durante 1997, no difirieron significativamente de los pesos registrados en los años sin El Niño, lo que sugiere que las aves fueron capaces de compensar una alimentación menor o menos frecuente de los pichones extendiendo el período de permanencia de los pichones en la cavidad. Consecuentemente, los pichones fueron también significativamente más viejos en el momento del alcanzar el peso máximo durante este evento cálido, lo que probablemente condujo a períodos prolongados de emplumamiento. Sin embargo, El Niño de 1997–1998 no afectó otros aspectos del comportamiento reproductivo de *C. monocerata*: la mortalidad de los pichones, aunque fue máxima en 1997, no fue significativamente diferente entre años; el número de intentos reproductivos fue similar entre años, como lo fue la sincronización temporal del período de cría. De este modo, debido a su biología reproductiva única, *C. monocerata* es capaz de adaptarse a las fluctuaciones climáticas del océano.

The most severe interannual fluctuations in marine ecosystems of the Pacific Ocean are El Niño events that occur on average every four years, although the interval between events has varied between two and

ten years (Cane 1983). The El Niño Southern Oscillation (ENSO) cycle involves an essential coupling between the atmosphere and the ocean, in which wind changes cause oceanic changes (Cane 1983). The first indications of an impending El Niño event usually come from the tropical Pacific Ocean. Along the eastern Pacific Rim El Niños manifest themselves with above-normal sea surface temperatures, a rise in sea level, and a deepening of the thermocline, the boundary between warm surface water and deeper cool water (Hamilton and Emery 1985, Norton et al. 1985). This destroys the local heat balance and there is little mixing of nutrient-rich, cool, deep water into the surface layer. As a result, primary production by phytoplankton in the euphotic zone becomes severely reduced due to nutrient depletion that disrupts the food web of higher-level marine organisms. A more detailed description of the ENSO phenomenon can be found in Barber and Chavez (1983), Cane (1983), Rasmussen and Wallace (1983), and Cane and Zebiak (1985).

Although the El Niño cycle has been known for several hundred years (Quinn et al. 1987), the 1982–1983 El Niño event, which at the time was hailed as the strongest in the 20<sup>th</sup> century, has focused considerable interdisciplinary research on this phenomenon. In California, adverse effects of the 1982–1983 El Niño on population dynamics of Least Terns (*Sterna antillarum*) have been documented (Massey et al. 1992), and in Oregon, Hodder and Graybill (1985) found that the 1982–1983 El Niño caused reduced reproductive success in Brandt's Cormorants (*Phalacrocorax penicillatus*), Pelagic Cormorants (*Phalacrocorax pelagicus*), and Common Murres (*Uria aalge*). The effects of the 1982–1983 El Niño on Alaskan seabirds were less clear (Hatch 1987). Examples of effects of El Niños on Washington's outer coast of the Olympic peninsula include: reduced numbers of Common Murres, Double-crested Cormorants (*Phalacrocorax auritus*), and Brandt's Cormorants at breeding colonies (Wilson 1991), and smaller clutches in marine Peregrine Falcons (*Falco peregrinus*, Wilson et al. 2000). However, much more research is needed before the effects of El Niños on the biology of seabirds can be fully appreciated.

A major seabird nesting area in Washington is comprised of the Strait of Juan de Fuca, the San Juan Islands, and Puget Sound. This area is oceanographically different from the outer coast and has been considered somewhat buffered from Pacific Ocean climatic fluctuations (Wilson and Manuwal 1986). In 1997 another severe El Niño rapidly developed, providing an opportunity to study the effects of El Niño on Rhinoceros Auklets (*Cerorhinca monocerata*) breeding on Protection Island. This study shows how the 1997–1998 El Niño event developed in Washington and how it affected Rhinoceros Auklets on Protection Island in the inner strait from two years prior to the onset of El Niño to two years after termination of the event.

#### METHODS

The effect of El Niño on breeding Rhinoceros Auklets was studied on Protection Island (48°08'N, 122°W), a part of Washington Maritime National Wildlife Refuge, in the Strait of Juan de Fuca (Fig. 1). The island's

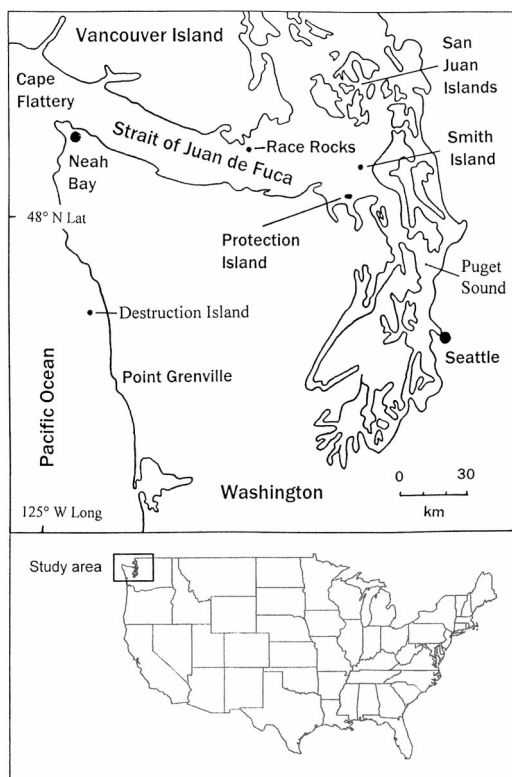


FIGURE 1. Map of Washington's marine areas with locations where Rhinoceros Auklet and El Niño data were collected.

breeding population of Rhinoceros Auklets was estimated at >17 000 pairs in 1975 (Wilson and Manuwal 1986) but has steadily declined to approximately 12 000 breeding pairs in 2000 (Wilson, unpubl. data). A much smaller colony on nearby Smith Island (Fig. 1) also suffered a similar decline (Wilson, unpubl. data). Protection Island (159 ha) hosts >70% of the seabirds breeding within Washington's inner coastal areas (Speich and Wahl 1989). The area around Protection Island is considerably more sheltered and drier than the outer coast, with an annual precipitation of

about 41 cm. Due to considerable tidal mixing, marine primary production in the inner strait does not depend on upwelling processes as much as on the outer coast (Wilson and Manuwal 1986).

To determine the presence of an El Niño event, I used monthly sea surface temperature anomaly charts for the U.S. west coast (NOAA 2000). In order to facilitate comparisons with previous work, I selected the same area of analysis for the Washington offshore waters (45°N to 50°N and seaward to 130°W) as in Wilson (1991). The charts are similar to topographic maps but instead of elevations show temperature anomalies in 0.5°C increments. From these charts, I calculated average monthly sea surface temperature anomalies for 1995–2000 by estimating the percentage of area covered by each temperature anomaly with a polar planimeter. The monthly anomaly is the difference between the monthly mean sea surface temperature and the climatological monthly mean value. The monthly mean sea surface temperature is derived from twice-weekly analyses using ship, buoy, and satellite observations, while the climatological mean value is derived from a database that extends back to 1965. Since the NOAA sea surface temperature anomaly charts do not include the Strait of Juan de Fuca and the waters around the San Juan Islands, I obtained monthly sea surface temperature data for Race Rocks (Fig. 1), (Fisheries and Ocean Canada 2002). The monthly sea surface temperatures for this location are the averages of the daily measurements for each month. I calculated monthly sea surface temperature anomaly values for this study using data back to 1965, the same period for which outer coast climatological means were derived. Sea level anomalies for Neah Bay, Washington (Fig. 1) were calculated by comparing the 1995–2000 monthly means to 30-year monthly averages extending back to 1965 (University of Hawai'i Sea Level Center 2001).

Artificial Rhinoceros Auklet burrows were used to study auklet breeding success. The burrows were constructed and maintained according to Wilson (1986). Artificial burrows resemble natural burrows and nesting birds have similar breeding success (Wilson 1986, 1993). At the start of this study, 45 artificial burrows that had been in operation since 1989 were used. Because of the loss of some burrows and the addition of new burrows, between 44 and 54 burrows were monitored annually during this study (Table 1). In each

TABLE 1. Summary of Rhinoceros Auklet reproductive data collected at Protection Island, Washington during 1995–2000.

Parameter	1995	1996	1997	1998	1999	2000
Number of artificial burrows monitored	45	44	54	53	50	50
Number chicks produced (% of burrows)	23 (51)	27 (61)	31 (57)	31 (58)	34 (68)	36 (72)
Number chicks that died in burrow	0	1	2	0	0	0
Mean hatch date	June 11	June 9	June 16	June 13	June 20	June 10
Age at peak weight (mean $\pm$ 95% CI)	45 $\pm$ 3	44 $\pm$ 2	48 $\pm$ 2	50 $\pm$ 1	44 $\pm$ 1	43 $\pm$ 1
Number of days between minimum and maximum weight (mean $\pm$ 95% CI) <sup>a</sup>	28 $\pm$ 3	27 $\pm$ 2	36 $\pm$ 2	37 $\pm$ 2	32 $\pm$ 2	24 $\pm$ 3

<sup>a</sup> This parameter was used to calculate chicks growth rates.



season of study, pairs produced between 23 and 36 chicks annually (Table 1). In order to avoid adults deserting eggs during incubation, the burrows were first checked for chicks toward the end of hatching. Chicks were weighed every 7–11 days thereafter with a Pesola spring scale and their wing chords were measured with a ruler. Because chicks were not measured daily, fledging weights and dates were not determined, and the peak weights (maximum mass) obtained in this study may not be the actual peak weights reached. I aged chicks by comparing their initial wing chord measurements with Protection Island data from Wilson and Manuwal (1986). For each chick, I calculated the overall average daily growth rate (weight gain) by dividing the difference between the maximum and minimum recorded weights by the number of days between the two measurements. This time interval varied between 28 and 37 days (Table 1). A one-way ANOVA, with years as a categorical variable, was used to analyze chick growth according to Zar (1984). Test results were considered significant at  $\alpha = 0.05$ .

## RESULTS

Wilson (1991) identified significant warm episodes affecting seabirds along the Washington outer coast as periods of four consecutive months when mean monthly sea surface temperature anomalies were a minimum of  $1^{\circ}\text{C}$ . During this study such a warming trend began in June 1997 on the outer coast (Fig. 2). Sea surface temperature anomalies were above  $1^{\circ}\text{C}$  for 9 of the next 11 months. Outer coast sea surface temperature anomalies during 1997 and 1998 were significantly higher than those of the other years of this study ( $U_{72} = 946$ ,  $P < 0.001$ ). This warming period was followed by a cold episode or La Niña event during the latter part of 1999, when negative sea surface temperature anomalies were recorded during six consecutive months (Fig. 2). The inner strait experienced similar warming during 1997–1998. Anomalies exceeding  $1^{\circ}\text{C}$  were first noted in August 1997 (Fig. 2). In 11 of the following 13 months, sea surface temperature anomalies were above  $1^{\circ}\text{C}$ . Similar to the outer coast, inner strait sea surface temperature anomalies during 1997 and 1998 were significantly higher than those of the other years of this study ( $U_{72} = 163$ ,  $P < 0.001$ ). There was a strong correlation between outer coast and inner strait sea surface temperature anomalies during 1995–2000 ( $r_s = 0.70$ ,  $n = 72$ ,  $P < 0.001$ ). Interestingly, there was no evidence of La Niña in the inner strait. Coincident with warm temperatures, the sea level anomaly at Neah Bay, Washington reached its highest level during January and February 1998 (Fig. 2). Monthly sea level anomalies during 1997 and 1998 were significantly higher than those of the other years of this study ( $U_{70} = 338$ ,  $P < 0.01$ ). Unfortunately, monthly data on thermocline depth were unavailable for Washington during this period.

Rhinoceros Auklet chick growth rates were lowest during the El Niño years of 1997 and 1998, with chicks born in 1997 having the slowest growth (Fig. 3). Significant differences were detected among years ( $F_5 = 11.3$ ,  $P < 0.001$ ), and pair-wise comparisons showed that the El Niño years of 1997 and 1998 were similar, and both were significantly different from non-

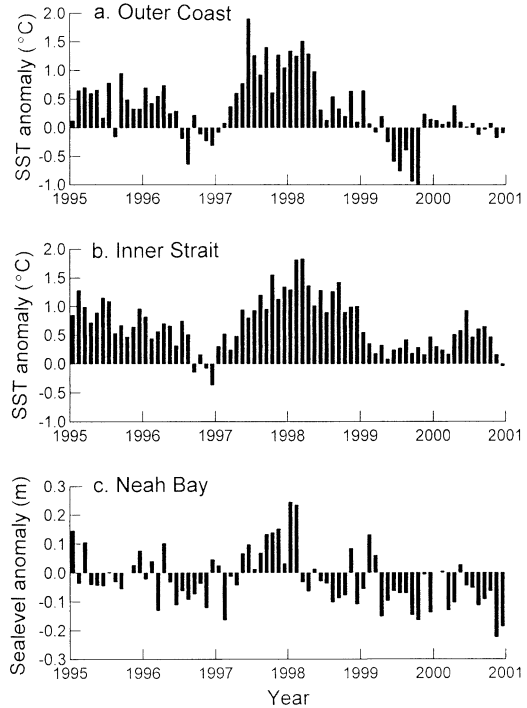


FIGURE 2. Monthly sea surface temperature (SST) anomalies (1995–2000) for (a) the Washington outer coast, (b) inner strait, and (c) monthly sea level anomalies for Neah Bay. The tick marks on the x-axis mark the beginning of the year, with the first month being January 1995.

El Niño years (Table 2). Overall, chick growth rates during El Niño years were 19% below normal years (Table 2). Because the chicks grew slower in 1997 and 1998, they were also significantly older at peak weight during these years ( $F_1 = 16.7$ ,  $P < 0.001$ ). This age difference of up to 7 days (Table 1), suggests that chicks had longer fledgling periods during El Niño years.

Although the chicks' peak weights were lowest in 1997 (Fig. 3), they were similar during all years ( $F_5 = 2.2$ ,  $P = 0.06$ ). The number of artificial burrows with chicks varied between 51% and 72% (Table 1) and was not significantly different among years ( $\chi^2_5 = 4.4$ ,  $P = 0.50$ ). Nestling mortality, although highest during 1997 (Table 1), was not significantly different among years ( $\chi^2_5 = 6.9$ ,  $P = 0.23$ ). The 1997–1998 El Niño also apparently did not affect the timing of the birds' breeding as mean hatching dates during the El Niño years were within the range of dates for normal years (Table 1).

## DISCUSSION

The 1997–1998 El Niño was prolonged and caused elevated sea surface temperatures and sea levels on Washington's outer coast and inner strait. Rhinoceros Auklets on Protection Island had lower chick growth rates and were older at peak weight during this El Niño



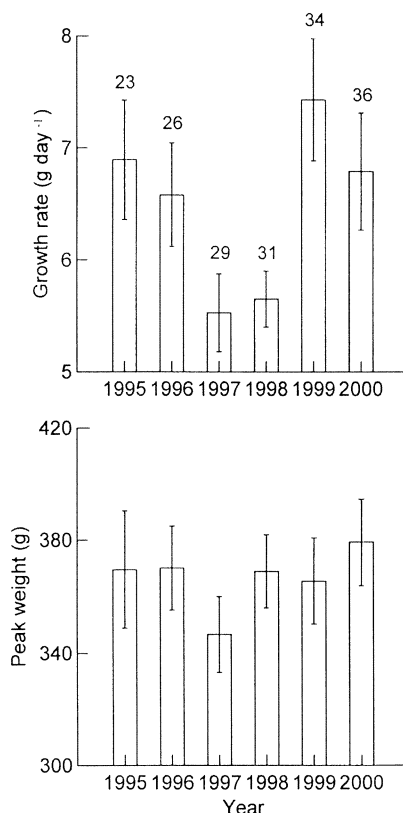


FIGURE 3. Nestling mean growth rates and mean peak weights with 95% confidence intervals of Rhinoceros Auklets on Protection Island, Washington, 1995–2000. Sample sizes are above the bars.

event. This El Niño did not affect other measures of birds' breeding.

In Washington the 1997–1998 El Niño event was unusual in that the period of warming was prolonged, even exceeding that of the 1983 El Niño, which at the time was considered the strongest of the century (Cane 1983). On the Washington outer coast sea surface temperature anomalies were a minimum of 1°C for nine months during 1997–1998, compared to only five months during the 1983 El Niño event (Wilson 1991). In 1997–1998 inner strait waters experienced warming similar in duration and magnitude as the outer coast, although the onset of warming was delayed two months in the inner strait. The 1997–1998 El Niño event was by some measures the strongest ever observed, as chlorophyll concentrations along the equatorial Pacific were the lowest ever recorded (Strutton and Chavez 2000). Eakin (1999) considered the 1997–1998 El Niño among the largest climate events experienced in modern times. Another major difference of this event was that anomalously warm water appeared on the west coast of North America before it could be forced by Kelvin wave advection from the south (O'Brien 1999).

TABLE 2. Matrix of Tukey pair-wise comparison probabilities of Rhinoceros Auklet chick growth rates from Protection Island, Washington during the years 1995–2000. Population means with 95% confidence intervals are listed below the table.

	1995	1996	1997	1998	1999
1996	0.95				
1997	<0.01	0.02			
1998	<0.01	0.05	1.00		
1999	0.60	0.09	<0.001	<0.001	
2000	1.00	0.99	<0.01	<0.01	0.27

$\mu_{1995, 1996, 1999, 2000}$ :  $6.9 \pm 0.2$  g day<sup>-1</sup>.

$\mu_{1997, 1998}$ :  $5.6 \pm 0.3$  g day<sup>-1</sup>.

$\mu_{1995, 1996, 1999, 2000} - \mu_{1997, 1998}$ :  $1.4 \pm 0.6$  g day<sup>-1</sup>.

The worst year for Rhinoceros Auklets on Protection Island was 1997 since birds had the slowest growth rates, the lowest peak weights, and chick mortality was higher than any other year of study, although the onset of significant warming did not occur until late in the breeding season (August) when 80% of the chicks had already reached their peak weights and were near fledging. During 1998, which experienced major warming during most of the breeding season, peak weights and nestling mortality of auklet chicks were comparable to normal years which suggests that environmental conditions for Rhinoceros Auklets in the inner strait deteriorated well before the measurable onset of the 1997–1998 El Niño and may have improved during the later phase of warming in 1998. The early deterioration of water conditions in the inner strait is likely due to the area being linked biologically to the outer coast where warming occurred two months earlier. The fact that chicks grew fastest during the 1999 La Niña event, although there was no physical evidence of a cold episode in the inner strait, also supports this idea since many seabirds frequently do well during cold water events (Boersma 1998).

Overall, Rhinoceros Auklets on Protection Island coped remarkably well with this El Niño event. Despite lower growth rates, chicks still attained peak weights similar to normal years suggesting that birds were able to compensate for either smaller or less frequent feedings by extending the time chicks were provisioned in the burrows. As a consequence, chicks were also older at peak weight during El Niño, which likely led to prolonged fledgling periods. We do not know if late fledging affected the survival of the chicks at sea. Because chicks were not weighed on a daily schedule, fledging weights, ages, and dates were not determined, and the peak weights obtained during this study were not necessarily the chicks' true peak nestling weights. With the exception of 1997, chicks mean peak weights were very close to the actual mean peak weights obtained on Protection Island in 1975 (371 g) and 1976 (369 g), when chicks were weighed daily (Wilson and Manuwal 1986). Chick growth rates are valuable data because they reflect the birds' environment (Ricklefs and White 1975); growth rates can be affected by environmental variation even when other

measures such as number of nests producing young, chick mortality, and peak nestling weights are not.

The findings that chick mortality and reproductive success (the number of burrows with chicks) were not significantly different in 1997–1998 vs. the non-El Niño years, and that hatch dates were similar in all years, is further evidence that this El Niño did not significantly handicap Rhinoceros Auklets in the inner strait. During the severe 1983 El Niño, Rhinoceros Auklets nesting at Destruction Island on the outer coast of Washington (Fig. 1) successfully reared young, at a time when murres and cormorants of the area were absent from their colonies (Wilson and Manuwal 1986, Wilson 1991). Thus, the unique biology of the Rhinoceros Auklet allows birds to cope with ocean environmental fluctuations easier than some other seabird species of this same region.

Rhinoceros Auklets breeding on the U.S. west coast have recently increased significantly in number, despite the recent period of ocean warming with more frequent severe El Niños and fewer La Niñas (Ainley et al. 1994, Boersma 1998). Auklets from Protection Island travel considerable distances within Washington's inner coastal waters in search for food (Wahl and Speich 1994). Since Rhinoceros Auklets are nocturnal with respect to colony visitation (Wilson and Manuwal 1986), they have considerable time during the extended daylight hours of summer in search of distant and patchy food supplies. Their nocturnal ability to catch food may also allow auklets to take advantage of diurnal vertical migration of marine prey organisms.

Since biological production of Washington's inner strait waters does not depend on upwelling for nutrient enrichment of the euphotic zone to the same extent of the outer coast, some researchers (Wilson and Manuwal 1986) speculate that the inner strait is somewhat protected from ocean climatic events. This study shows that during strong El Niños the inner strait experiences similar warming to the outer coast, and that strong El Niños can significantly impact Strait of Juan de Fuca Rhinoceros Auklet chick growth rates and thus extend the time it takes for chicks to reach their peak weights.

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